

IMMOBILIZATION OF MINERAL NUTRIENTS BY PHILOSCIA MUSCORUM  
(ISOPODA, ONISCOIDEA) IN A DUNE GRASSLAND ECOSYSTEM

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ИММОБИЛИЗАЦИЯ МИНЕРАЛЬНЫХ БИОГЕНОВ МОКРИЦЕЙ PHILOSCIA MUSCORUM (ISOPO-  
DA, ONISCOIDEA) В ЛУГОВОЙ ЭКОСИСТЕМЕ ДЮНЫ

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Introduction

Assessing "the role of soil animals in soil fertility", the theme of this colloquium, is a very difficult problem. This is partly because "soil fertility" is an ecosystem parameter defined in relation to the total primary production of the whole assemblage of plants growing in that soil, and thus affected by the extent to which each individual species of plant is adapted to conditions of high or low nutrient availability. Ecosystem parameters can be described in physical and chemical terms, but because ecosystems do not evolve as functional units, we cannot apply the most powerful, generalized principles of Biology, namely evolutionary theories, to understanding problems concerning the parameters of whole ecosystems.

Selection pressures, which ultimately determine the role of any organism in any ecosystem, operate not at the level of whole ecosystems nor on whole communities within them, nor even on trophic groups such as saprophagous soil animals, but on individuals. A characteristic of individuals is that they vary enormously not only between populations of one species but also within populations with age, sex and time. In order to obtain true biological insight and understanding of "The role of soil animals in soil fertility" we have to take account of this variability. This paper describes variability in the extent to which the isopod Philoscia muscorum (Scopoli) im-

mobilizes mineral nutrients in a sand-dune ecosystem and hence dampens fluctuations in their release from decaying leaf litter.

The influence of any soil organism on soil fertility will depend upon how it affects the balance between the simultaneous processes:

Mineralization  $\rightleftharpoons$  Immobilization

Most previous studies of soil animals, as reviewed by /12/ and /16/, have concentrated on their contributions to mineralization. Some, e.g. /13/ have compared concentrations of nutrients in saprophagous animals and leaf litter but relatively few, with the notable exception of /8,9/, have studied rates of immobilization by animals. The biological immobilization of nutrients is most important in soils which have a low cation exchange capacity due to having few physical buffers in the form of humus and clay mineral particles. Such soils are found in sand-dune ecosystems where the mineral component consists entirely of recently blown sand and the humus has not yet accumulated. Fertility in these soils is greatly reduced by rapid leaching of mineral nutrients immediately after their release from plant litter. Hence any nutrients which are incorporated into animal biomass have an important buffering effect in dampening the annual fluctuations in nutrient release from decaying leaf litter.

In the dune grassland described by /15/ *Philoscia muscorum* is the most conspicuous member of the soil fauna occurring at densities of approximately 400 m<sup>-2</sup>. To assess its contribution to nutrient immobilization very detailed estimates of the rates of biomass accumulation by different age, and sex groups in the population are combined with analyses of the nutrient content of the tissues of these subgroups.

#### Materials and Methods

Density, Growth and Population Production. 14 x 0.1 m<sup>-2</sup> samples were taken on a stratified random basis from the 441 m<sup>2</sup> study site at approximately 2 monthly intervals from 1968 until 1973. Animals were collected using a high gradient extractor and their density and size frequency analysed as described in /15/. Four sub-groups could be identified in the population: immatures, males, fast-growing females and slow-growing females. Growth rates were determined for each sub-group of each cohort by quantifying the relationship between live weight and headwidth for each sub-group and using the resulting regression equations to determine their mean weights on each sampling date. By combining these with the estimates of sub-group density on each date, growth-survivorship curves were plotted and from these population production by each sub-group estimated. The relationship between live and dry weight was determined by drying samples to constant weight at 60° under vacuum. The ash contents of samples was determined by burning them in a muffle furnace at 500° for 4 hours.

Nutrient Content. Dried and ground samples of ash were dissolved in 3 ml of 8 N nitric acid at 95° for 2 hours made up to 50 ml with deionized water, filtered and analysed using a Pye Unicor S.P.9 atomic absorption spectrophotometer operated in the flame mode. All glassware was soaked for 24 hours in 4 N nitric acid and triple rinsed in double distilled water and then deionized water.

#### Results

Considerable variation in the concentration of all five of the elements analysed is shown by the preliminary data presented in Table 1. Further replication will be required to establish the statistical significance of some of the observed differences but consistent trends are already apparent. In particular the concentration of all five elements in the young on release from the brood pouch was on average 5.6 x greater, ranging from 1.5 x greater for calcium to 17.2 x greater for copper than in the adult males and females. For sodium and copper, where the differences are most marked, higher levels persist into the immature stage. The total ash content is also higher in the younger stages which is partly because a large proportion of the ash is derived from the exoskeleton. As the surface area to volume ratio decreases with increased size the proportion of exoskeleton to other body tissues also decreases, hence reducing the proportion of ash. However this does not explain all of the differences in concentration of elements between young and adults as when the results are expressed in concentrations of elements per unit weight of ash there is still on average 3.1 x as much present in the newly emerged young as there is in the adult female parents.

Analysis of seasonal variation with females that are not carrying brood pouches shows that some elements such as calcium build up from a low concentration of 83.8 mg.g<sup>-1</sup> D.W. in Winter to 96.6 mg.g<sup>-1</sup> in Spring and then a peak of 104.7 mg.g<sup>-1</sup> just prior to breeding in Summer dropping back to 97.5 mg.g<sup>-1</sup> after the release of the broods. This suggests that the females are selectively provisioning the young with mineral nutrients which may otherwise be difficult for them to obtain in adequate amounts for constructing their exoskeletons during the first very rapid growth phase.

For both potassium and calcium there are also significant differences between the two sexes, in both cases adult males have higher concentrations than the females even during the females' pre-reproductive peak.

Of the five elements analysed calcium concentrations are consistently the highest by an order of magnitude. This can be accounted for by the high requirement that all crustaceans have for this element to construct their calcareous exoskeletons. The concentrations in the isopod tissue were 4.3 x higher than in the amorphous litter, the very small fragments of extensively decayed litter found at the interface between the litter layer and soil profile in this system, and shown in food preference tests to be the most preferred of the foods available /1/. Magnesium and potassium were also present at significantly higher levels in the adult isopod's tissues than in their food but this was not the case for sodium which was five times more concentrated in the food than was potassium, probably due to the influence of salt spray from the sea which is only approximately 100 m. from the site at high tide.

All the elements were more concentrated in the food than in faeces that had been collected from the animals in the field as described in /2/.

In order to estimate rates of immobilization these data concerning concentrations of nutrients have to be combined with estimates of the rates at which the isopod tissues are accumulated by the field populations. Because

Table 1. Variation in nutrient content of *Philoscia muscorum* tissue with age and sex

Cohort Sub-group	Number of Analyses	Concentration of element (mg.g <sup>-1</sup> dry wt.)					
		$\bar{x} \pm 1 \text{ S.E.}$					
		Na	K	Ca	Mg	Cu	Total Ash
Young at release	1	59.8	10.1	177.7	6.4	10.3	427
							$\pm 45.5$ (2)
Immatures	3	18.1	5.8	101.8	3.2	2.6	337
		$\pm 2.75$	$\pm 0.25$	$\pm 3.03$	$\pm 0.15$	$\pm 0.42$	$\pm 4.1$ (6)
Males	2	10.4	7.6	140.1	3.9	0.3	309
		$\pm 0.06$	$\pm 0.57$	$\pm 4.76$	$\pm 0.25$	$\pm 0.02$	$\pm 10.0$ (4)
Females	4	9.9	4.7	95.7	3.3	0.9	292
		$\pm 0.79$	$\pm 0.41$	$\pm 4.34$	$\pm 0.32$	$\pm 0.43$	$\pm 7.4$ (5)
Food (amorphous leaf litter)	3	11.8	2.2	27.2	2.1	1.6	516
		$\pm 1.44$	$\pm 0.05$	$\pm 3.53$	$\pm 0.08$	$\pm 0.28$	$\pm 33.6$ (5)
Faeces	2	3.2	1.1	13.1	0.9	1.2	249
		$\pm 1.46$	$\pm 0.16$	$\pm 7.17$	$\pm 0.19$	$\pm 1.09$	$\pm 12.3$ (5)

of the differences in concentration in the different sub-groups it is clear that biomass accumulated by the different groups must be calculated separately. By combining the mean size and mean density data obtained from the sampling programme for each sub-group into a series of growth-survivorship curves /10/ population production estimates were obtained as shown in column 1 of Table 2 for the specimen year August 1971 to August, 1972. This year was chosen as population production was particularly high then due largely to a very big contribution, 56% of the total, made by the immatures following a particularly high recruitment in July/August 1971. As shown above the concentrations of some elements in the immatures is very much higher than in other groups so when over half of the population production is contributed by this group it is very important to use the appropriate concentrations if a reasonably accurate estimate of immobilization rates is to be obtained.

The contribution of the different sub-groups to total immobilization of each element is shown in Table 2 and the mean rates for each element over the 5 year study period in the top row of Table 3. These data show very clearly that rates of immobilization are greatest for calcium which is accumulated in isopod biomass to more than 6 x the extent of any of the other elements. It is interesting that 3 x more sodium is accumulated than potassium which may be related to the high concentrations in the food and the need to maintain the right balance of concentrations across the gut epithelium. The rates of accumulation of copper are perhaps greater than might be expected for what is normally a trace element, but this is related to isopod's well known requirement for copper to produce haemocyanin and their enormous capacity for storing this element in the hepatopancreas /17, 18/.

The rates at which this population egest faecal material have been very thoroughly investigated in /1,2/. By combining his estimates of egestion

Table 2. Population production and nutrient immobilization by *Philoscia muscorum* during 1971/72 (mg. m<sup>-2</sup> yr<sup>-1</sup>)

Cohort Sub-group	Population Production (Mg. D.W.)	Immobilization of				
		Ca	Na	K	Mg	Cu
Young at release	156	27.7	9.3	1.6	1.0	1.6
Immatures	1294	131.7	23.1	7.5	4.1	3.4
Males	293	41.1	3.1	2.2	1.1	0.1
Females	553	52.9	5.4	2.6	1.8	0.5
Totals	2296	253.4	40.9	13.9	8.0	5.6

Table 3. Average nutrient budget for *Philoscia muscorum* during 1968-1973 (mg. g<sup>-2</sup> yr<sup>-1</sup>)

Parameters of energy budget	Ca	Na	K	Mg	Cu	Total Ash
Assimilation (A)	168.6	27.7	9.2	5.4	3.7	486.7
Egestion (FU)	504.8	124.5	40.5	35.8	46.7	9578.9
Consumption (A + FU)	673.4	152.2	49.7	41.2	50.4	10065.6
Efficiency Assimilation (%)	25.0	18.2	18.5	13.1	7.4	4.8%

rate with the data on nutrient contents of the faeces it is possible to determine the rate at which each element is egested by this population in the field while feeding on their natural diet of a mixture of decaying plant remains. These estimates are shown in row 2 of Table 3. From these data it is possible to construct a nutrient budget, analogous to an energy budget such as the one presented for this population in /5/. Because there are no respiratory losses of these nutrients and all excretory losses are taken into account by analysis of the faeces, the population production term of the budget becomes equivalent to the assimilation term. Thus if rates of immobilization (equivalent to population production) and hence assimilation rates are combined with egestion rates, the rates at which each element was consumed can be calculated as shown in row 3 of Table 3. Similar calculations for the energy budget showed that this one species of decomposer alone consumed approximately 5.4% of the litter input into this sand-dune soil system /5/.

The assimilation and consumption rates can be used to calculate assimilation efficiencies as shown in the final row of Table 3. It is of interest to note that except for calcium all of these are lower than the assimilation efficiency for energy of 19.3% /5/.

## Discussion

The above data do not give a direct estimate of the role of P. muscorum in fertility of this developing sand dune soil because that would require detailed knowledge of how plant nutrient requirements varied with time, the concentrations of the elements in the soil solution at the times of peak demand, and the rates and pathways of nutrient release from dead isopod tissue. However it is clear from these results that substantial quantities of these elements are immobilized by being incorporated into isopod biomass, thus their retention in this immature soil is prolonged so increasing the probability of their being reabsorbed by the plants.

While these conclusions could possibly have been reached as a result of a less detailed study, by analysing the different sub-groups of the population separately, considerable biological insight has been obtained into reasons for variation in nutrient content with the age and sex of the animals. The provisioning of their young with stores of mineral nutrients has not previously been reported for isopods and implies, particularly in view of the low levels of assimilation efficiency for the population overall, that the young have a particularly high requirement for mineral nutrients which could be an important limiting factor as it was concluded in /6/ for the study of herbivorous grasshoppers and the omnivorous cricket Pteronemobius fasciatus in another grassland ecosystem.

Furthermore the big difference in concentrations of nutrients between sub-groups has to be taken into account, in view of the big variation in their contributions to total production, if reliable totals for calculating assimilation efficiencies are to be obtained.

The assimilation efficiency data provide a means of testing one of the most stimulating and provocative hypotheses to have been generated as a result of the study of whole ecosystems. In /14/ proposed that ecosystem functions were limited not by the supply of energy but by the availability of nutrients. This argument was supported by evidence that most trophic groups processed energy wastefully in order to acquire and conserve adequate supplies of mineral nutrients. Evidence from laboratory studies of isopods appeared to confirm this: in /11/ it was shown that cesium-134 was absorbed with efficiencies of up to 87% and in /7/ that strontium-90 was absorbed with efficiencies of up to 80% while it was known from this and other studies that isopods normally only absorb about 20% of the energy they ingest.

The present study of a population ingesting its natural diet in situ in the field reveals that for the natural isotopes of mineral nutrients assimilation efficiencies are lower for the nutrients than they are for energy.

This is even true for copper which in the past has been thought to be a critically limiting nutrient (but see /3,4/). The only one of these five nutrients absorbed more efficiently than energy is calcium for which, as explained above, they have an exceptionally high requirement. Thus it would seem that these data do not support /14/ hypothesis. It must however be remembered that this is not a complete nutrient budget as several important elements, notably phosphorus and nitrogen were not analysed. In /4/ it is clearly shown that the concentrations of nitrogen in isopod foods have a

marked effect on their fitness so it could well be that both energy and these other normal nutrients are being processed wastefully in order to obtain adequate amounts of ~~this~~ critically limiting elements.

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#### D i s c u s s i o n

Petersen H.: Do you have an explanation of the higher mineral concentrations observed in juveniles compared to adults, or is this phenomenon known for other animal groups?

Hassall M.: I cannot yet explain the higher concentrations in juveniles. I do not think that it is simply a result of allometric growth patterns as the concentrations per unit weight of ash are higher as well as the ash content itself being higher. It is possible that the parents are provisioning their young with a large supply of critical nutrients which the young may be less well able to equip themselves. Seasonal differences in calcium content, for example, in the females suggest that this could be so as calcium concentrations peak in females before breeding drops to a minimum just after brood release. I am not aware of this having been shown for other groups of animals.

I am aware that there are differences in feeding behaviour between immatures and adults, as for example immatures appear to have a much greater need to recycle faeces than adults. I do not yet know which nutrients they are obtaining more readily by this increased coprophagous behaviour.

Marialigeti K.: Would you tell us something about the distribution of the accumulated elements in the body of the investigated isopod.

Hassall M.: I have not looked at the localization of these nutrients in detail in Philoscia muscorum except that histological studies revealed large concentrations of copper in the hepatopancreas and of iron in the hepatopancreas and the hind gut wall. Dr. S.Hopkins has found that metals such as zinc and cadmium are also concentrated in the hepatopancreas of Oniscus asellus. Calcium is most concentrated in the exoskeleton.

Striganova B.R.: What factors determine slow and fast growth patterns of female Philoscia muscorum?

Hassall M.: These appear to be determined by interactions between temperature, body size and the timing of brood release. Broods which are released early in the summer grow very rapidly due to the higher temperatures. Broods re-

leased later, towards the end of the summer, are more strongly affected by the colder temperature during autumn, winter and early spring because they are smaller and so are unable to grow fast enough to breed in their first year. They then grow rapidly during their second summer to become very large by the time they breed when two years old.

The question: You have described the accumulation of nutrients isopod biomass. Could you tell us anything about the subsequent fate?

Hassall M.: Nutrients are taken out of the population when the animals die and for this population mortality is highest during the juvenile stages when over 10% of the cohort is predated by spiders, centipedes and beetle larvae (Sunderland, Sutton, 1981). Observations made by Dr.Sunderland also showed that any dead P.muscorum is rapidly eaten by scavenging invertebrates particularly ants. A proportions of the nutrients are thus incorporated into predator and scavenger biomass and the undigested rests - into predator or scavenger faeces.